ZooKeys 1243: 269–288 (2025)
DOI: 10.3897/zookeys.1243.152263

Research Article

A new species of *Ptychognathus* Stimpson, 1858, from East and Southeast Asia, previously identified as *Ptychognathus barbatus* (A. Milne-Edwards, 1873) (Crustacea, Decapoda, Brachyura, Varunidae)

Jhih-Wei Hsu[1], Jose Christopher E. Mendoza[2], Hsi-Te Shih[1,3]

1 *Department of Life Science, National Chung Hsing University, Taichung 402, Taiwan*
2 *Lee Kong Chian Natural History Museum, Faculty of Science, National University of Singapore, 2 Conservatory Drive, 117377 Singapore, Singapore*
3 *Global Change Biology Research Center, National Chung Hsing University, Taichung 402, Taiwan*

Corresponding author: Hsi-Te Shih (htshih@dragon.nchu.edu.tw)

Abstract

The brackish-water crabs of the genus *Ptychognathus* Stimpson, 1858, currently the most diverse genus within the family Varunidae, typically inhabit estuaries or seashores influenced by freshwater. Among the species in this genus, a commonly recorded species identified as *Ptychognathus barbatus* (A. Milne-Edwards, 1873) has been recorded across the western Pacific, including Japan, Taiwan, China, the Philippines, Malaysia, Indonesia, and New Caledonia (type locality). However, some previous studies suggested that most of these records do not represent the true *P. barbatus*. The present study reexamines these records and specimens and describes a new species, *P. dajie* **sp. nov.**, from East and Southeast Asia, based on morphological differences and genetic data from mitochondrial cytochrome c oxidase subunit 1 (COI). This new species is similar to its congeners but can be distinguished by the features of the carapace, the setation of ambulatory legs, and male first gonopods. In addition, the intraspecific distances of *P. dajie* **sp. nov.** are below 0.77%, while the interspecific distances between this new species and other species are larger than 11.89%.

Key words: description, mitochondrial cytochrome c oxidase subunit I, morphology, *Ptychognathus dajie* sp. nov.

OPEN ACCESS

Academic editor: Sameer Pati
Received: 7 March 2025
Accepted: 25 April 2025
Published: 27 June 2025

ZooBank: https://zoobank.org/6E0DB5CB-73B5-4C61-9CC1-6C69611093EA

Citation: Hsu J-W, Mendoza JCE, Shih H-T (2025) A new species of *Ptychognathus* Stimpson, 1858, from East and Southeast Asia, previously identified as *Ptychognathus barbatus* (A. Milne-Edwards, 1873) (Crustacea, Decapoda, Brachyura, Varunidae). ZooKeys 1243: 269–288. https://doi.org/10.3897/zookeys.1243.152263

Copyright: © Jhih-Wei Hsu et al.
This is an open access article distributed under terms of the Creative Commons Attribution License (Attribution 4.0 International – CC BY 4.0).

Introduction

Ptychognathus Stimpson, 1858, is currently the most speciose genus within the family Varunidae H. Milne Edwards, 1853, with a wide distribution across the Indo-West Pacific. To date, a total of 32 species of *Ptychognathus* have been described (Sasaki 2023; Hsu and Shih 2024a; De Mazancourt et al. 2024; Patel et al. 2025). Although the genus has a broad distribution, most species are distributed in the western Pacific region (Hsu et al. 2022; Sasaki 2023; De Mazancourt et al. 2024); and several recently described species of *Ptychognathus* are also from this area (e.g., *P. lipkei* NK Ng, 2010; *P. makii* Hsu & Shih, 2020; *P. stimpsoni* Hsu & Shih, 2020; and *P. sakaii* Hsu, Shih & Li, 2022). In this

highly diverse region, some studies suggested that there are still undescribed species of this genus (Hsu and Shih 2020).

Ptychognathus barbatus (A. Milne-Edwards, 1873) was originally described as *Gnathograpsus barbatus* A. Milne-Edwards, 1873, based on specimens from New Caledonia (see A. Milne-Edwards 1873). This species was subsequently recorded in several localities, including many areas of East and Southeast Asia, such as China, Japan, Taiwan, Malaysia, and Indonesia (De Man 1895, 1902; Sakai 1939, 1976; Dai et al. 1986; Dai and Yang 1991; Sasaki 2023). Recent studies (Hsu and Shih 2020; Hsu et al. 2022), however, have indicated that many of the records of "*Ptychognathus barbatus*" from East and Southeast Asia do not represent the true *P. barbatus*, but rather, is an undescribed species (see Ng 2006). In her unpublished doctoral thesis, Ng (2006) undertook a systematic revision of the entire family Varunidae, including the genus *Ptychognathus*. Therein she established a new genus, "*Cognatus*", under which she included two new species from East and Southeast Asia, viz. "*Cognatus cavaterminus*", from China, Japan, Taiwan, Philippines, Indonesia, Malaysia, and "*C. benokiensis*", from the Ryukyu Islands (Ng 2006: 384). As the taxonomic and nomenclatural acts in NK Ng's thesis were indicated as unpublished (see Disclaimer in thesis, p. xiii), the names of these new taxa are considered unavailable in accordance with Articles 8 and 10 of the International Code of Zoological Nomenclature (ICZN 1999). For the present study, an opportunity to validate and update the work of Ng (2006) work has presented itself. Examination of her material, as well as additional material from East and Southeast Asia previously identified as *P. barbatus*, and topotypic material of *P. barbatus* sensu stricto, confirms that the relevant records of "*P. barbatus*" from the region and the species placed in "*Cognatus*" by NK Ng have the sufficient morphological and molecular distinctions to be recognized as a new species of *Ptychognathus*.

In recent years, several studies on *Ptychognathus* have used molecular analyses to assist in species differentiation, demonstrating that the COI (cytochrome *c* oxidase subunit I) gene is useful for the classification and identification of most *Ptychognathus* species. This marker has also been effective in confirming more significant intraspecific morphological variation in some species (Hsu and Shih 2020, 2024a; De Mazancourt et al. 2024). Therefore, present study used COI to aid in the identification of this new species and to check intraspecific and interspecific morphological variation.

Materials and methods

The examined specimens are deposited in the Zoological Collections of the Department of Life Science, National Chung Hsing University, Taichung, Taiwan (**NCHUZOOL**), and the Zoological Reference Collection of the Lee Kong Chian Natural History Museum, National University of Singapore (**ZRC**). The collection sites of the specimens are shown in Fig. 1.

The following abbreviations are used in present study: **CW** = carapace width, **CL** = carapace length; **P2–P5** = first to fourth ambulatory legs; **G1** = male first gonopod; **G2** = male second gonopod; **ovig**. = ovigerous.

Genomic DNA was isolated from the muscle tissue of legs, gills, or eggs by using the GeneMark tissue and cell genomic DNA purification kit (Taichung, Taiwan). A portion of the COI gene was amplified with PCR using the primers

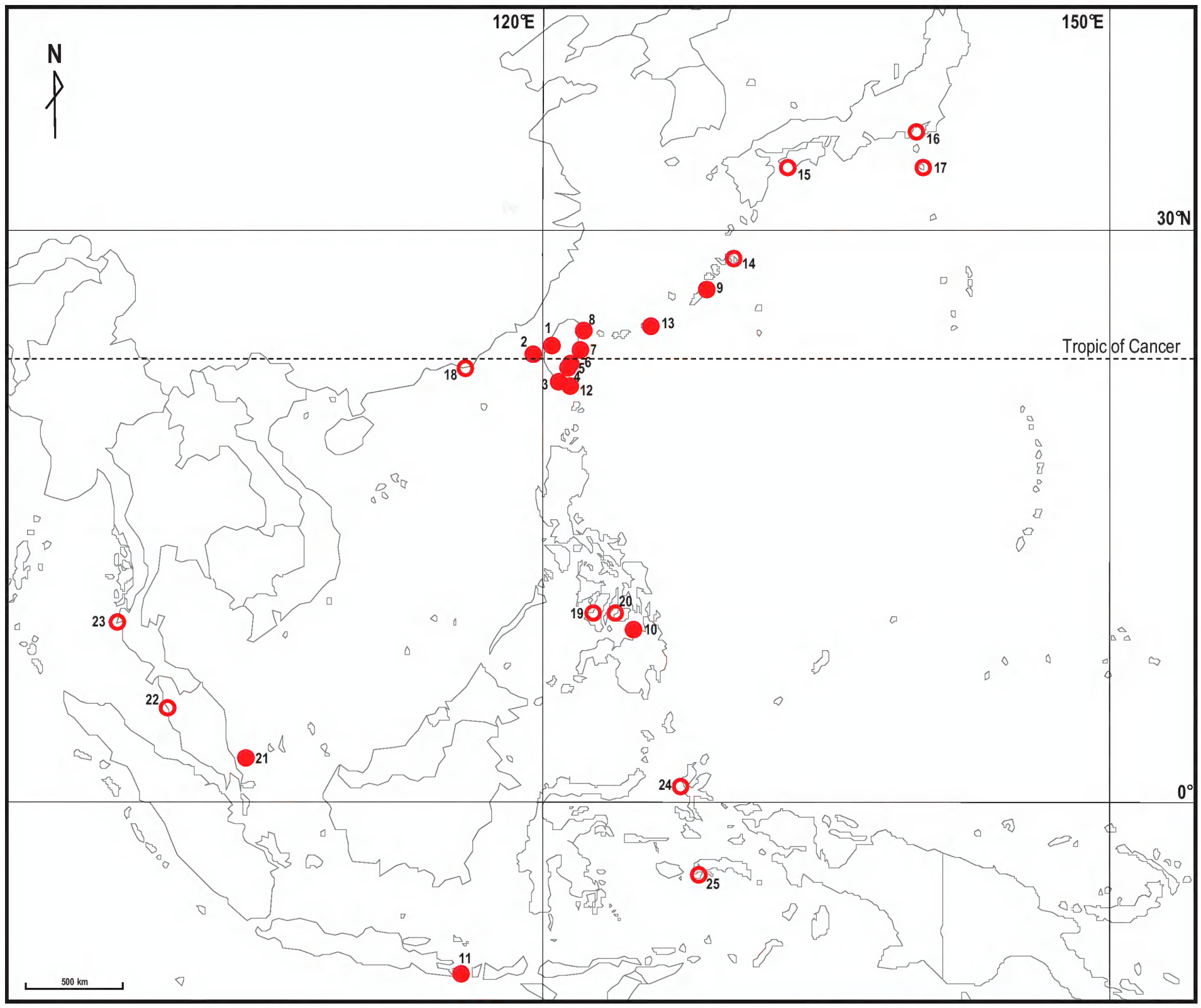

Figure 1. The collection sites of *Ptychognathus dajie* sp. nov. in East and Southeast Asia. Solid symbols mean collection sites of specimens used in present study; empty symbols mean the additional records only from references. 1–11 refer to Table 1; 12, Lanyu Island, Taiwan; 13, Miyako Islands, Japan; 14, Amami Island, Japan; 15, Kochi and Ehime, Japan; 16, Kanagawa, Japan; 17, Izu Islands, Japan; 18, Guangdong, China; 19, Negros, the Philippines; 20, Cebu, the Philippines; 21, Tioman Island, Malaysia; 22, Penang, Malaysia; 23, Phuket, Thailand; 24, Ternate, Indonesia; 25, Ambon Island, Indonesia.

LCO1490 (5'-GGTCAACAAATCATAAAGATATTGG-3'), HCO2198 (5'-TAAACTTCAGGGTGACCAAAAAATCA-3') (Folmer et al. 1994), LCOB (5'-CAAAYCATAAAGAYATYGG-3'), and HCOex3 (5'-GCTCANACTACRAATCCT A-3') (Shih et al. 2022). The PCR conditions for the above primers were denaturation for 50 s at 94 °C, annealing for 70 s at 45–47 °C, and extension for 60 s at 72 °C (40 cycles), followed by extension for 10 min at 72 °C. Amplicon sequences were obtained using an automated 3730 Series DNA Analyzer (Applied Biosystems, Foster City, CA, USA) after verification with the complementary strand. Haplotype sequences have been deposited in the GenBank database, and their accession numbers are listed in Table 1. The molecular analyses also included other haplotypes from GenBank published in Hsu and Shih (2020, 2024a, 2024b), Winarni et al. (2023), and De Mazancourt et al. (2024).

A neighbor-joining (NJ) tree for COI sequences was constructed using the Kimura (1980) 2-parameter (K2P) model with the 2,000 bootstrap reiterations and complete deletion option in MEGA (v. 11, Tamura et al. 2021).

Table 1. The haplotypes of the cytochrome c oxidase subunit I (COI) for the specimens of *Ptychognathus* species used in present study. The numbers in parentheses following the localities indicate the collection sites, corresponding to those shown in Fig. 1.

Species	Locality	Sample size	Accession number	References
P. dajie sp. nov.	Taiwan: Fubao, Changhua [1]	1	MW000767	Hsu and Shih (2020)
	Taiwan: Watong, Baisha, Penghu [2]	1	MW000768	Hsu and Shih (2020)
	Taiwan: Baoli R. estuary, Pingtung [3]	1	MW000768	Hsu and Shih (2020)
	Taiwan: Dulanwan, Taitung [4]	1	MW000767	Hsu and Shih (2020)
	Taiwan: Shanyuan, Taitung [5]	1	MW000768	Hsu and Shih (2020)
	Taiwan: Shanyuan, Taitung [5]	1	MW000767	Hsu and Shih (2020)
	Taiwan: Jihuei, Taitung [6]	1	MW000767	Hsu and Shih (2020)
	Taiwan: Yanliao, Hualien [7]	1	MW000769	Hsu and Shih (2020)
	Taiwan: Dasi R. estuary, Yilan [8]	1	MW000767	Hsu and Shih (2020)
	Japan: Benoki, Okinawa Island [9]	1	PV557377	present study
	Philippines: Camiguin Island [10]	1	MW000770	present study
	Indonesia: Bali [11]	1	MW000770	Hsu and Shih (2020)
P. guijulugani	Indonesia: Bali	1	PV557376	present study
P. pusillus	Australia: Dolly Beach, Christmas Island	1	PP294706	Hsu and Shih (2024a)
P. amikee	Vanuatu: Kirilou River, Gaua Island	1	PP294699	Hsu and Shih (2024a)
	Vanuatu: Kirilou River, Gaua Island	1	PP294700	Hsu and Shih (2024a)
P. takahasii	Taiwan: Jihuei, Taitung	1	MW000786	Hsu and Shih (2020)
P. insolitus	Taiwan: Houwan, Pingtung	1	MW000774	Hsu and Shih (2020)
	Taiwan: Houwan, Pingtung	1	MW000775	Hsu and Shih (2020)
P. similis	Wallis & Futuna (France): Futuna Island	1	OR864756	De Mazancourt et al. (2024)
	Wallis & Futuna (France): Futuna Island	1	OR864757	De Mazancourt et al. (2024)
P. hachijoensis	Taiwan: Chaishan, Kaohsiung	1	MW000771	Hsu and Shih (2020)
	Taiwan: Houwan, Pingtung	1	MW000772	Hsu and Shih (2020)
	Taiwan: Jioupeng, Pingtung	1	MW000773	Hsu and Shih (2020)
P. ngankeeae	Wallis & Futuna (France): Futuna Island	1	OR864752	De Mazancourt et al. (2024)
	Wallis & Futuna (France): Futuna Island	1	OR864753	De Mazancourt et al. (2024)
P. barbatus	New Caledonia: Grande Terre Island	1	OR864745	De Mazancourt et al. (2024)
P. stimpsoni	Taiwan: Wanlitong, Pingtung	1	MW000782	Hsu and Shih (2020)
	Philippines: Camiguin	1	MW000784	Hsu and Shih (2020)
	Philippines: Camiguin	1	MW000783	Hsu and Shih (2020)
	Philippines: Camiguin	1	MW000785	Hsu and Shih (2020)
P. sakaii	Taiwan: Dingtanzih, Pingtung	2	MW000787	Hsu and Shih (2020)
P. lipkei	Taiwan: Yeyin, Lanyu Island	1	PP294702	Hsu and Shih (2024a)
	Taiwan: Yeyin, Lanyu Island	1	PP294703	Hsu and Shih (2024a)
	Taiwan: Yeyin, Lanyu Island	1	PP294704	Hsu and Shih (2024a)
P. glaber	Japan: Ogasawara (Bonin)Islands	1	PP272962	Hsu and Shih (2024b)
P. ishii	Taiwan: Dulanwan, Taitung	1	MW000778	Hsu and Shih (2020)
	Taiwan: Gangkou R. estuary, Pingtung	1	MW000776	Hsu and Shih (2020)
	Taiwan: Gangkou R. estuary, Pingtung	1	MW000777	Hsu and Shih (2020)
P. riedelii	Philippines: Cebu Island	1	PP294705	Hsu and Shih (2024a)
	Philippines: Cebu Island	1	PP272963	Hsu and Shih (2024b)
P. pilosus	Taiwan: Gangkou R. estuary, Pingtung	1	MW000781	Hsu and Shih (2020)
P. altimanus	Taiwan: Gangkou R. estuary, Pingtung	1	MW000764	Hsu and Shih (2020)
	Taiwan: Linbian R. estuary, Pingtung	1	MW000765	Hsu and Shih (2020)
	Indonesia: Cilacap, Central Java	1	OQ852797	Winarni et al. (2023)
	Taiwan: Gangkou R. estuary, Pingtung	1	MW000763	Hsu and Shih (2020)
	Taiwan: Linbian R. estuary, Pingtung	1	MW000766	Hsu and Shih (2020)
P. makii	Taiwan: Gangkou R. estuary, Pingtung	1	MW000779	Hsu and Shih (2020)
	Taiwan: Gangkou R. estuary, Pingtung	1	MW000780	Hsu and Shih (2020)

Species	Locality	Sample size	Accession number	References
P. crassimanus	French Polynesia: Fatu Hiva Island	1	OR864744	De Mazancourt et al. (2024)
	French Polynesia: Fatu Hiva Island	1	OR864760	De Mazancourt et al. (2024)
	French Polynesia: Fatu Hiva Island	1	OR864759	De Mazancourt et al. (2024)
	French Polynesia: Fatu Hiva Island	1	OR864751	De Mazancourt et al. (2024)
	French Polynesia: Fatu Hiva Island	1	OR864742	De Mazancourt et al. (2024)
	French Polynesia: Fatu Hiva Island	1	OR864750	De Mazancourt et al. (2024)
P. easteranus	French Polynesia: Tahiti	1	OR864766	De Mazancourt et al. (2024)
	French Polynesia: Tahiti	1	OR864767	De Mazancourt et al. (2024)
	French Polynesia: Mangareva Island	1	OR864763	De Mazancourt et al. (2024)
	French Polynesia: Rapa Island	1	OR864755	De Mazancourt et al. (2024)
	French Polynesia: Rapa Island	1	OR864765	De Mazancourt et al. (2024)
	French Polynesia: Tahiti	1	OR864748	De Mazancourt et al. (2024)
	French Polynesia: Rurutu Island	1	OR864746	De Mazancourt et al. (2024)
	French Polynesia: Tahiti	1	OR864749	De Mazancourt et al. (2024)
	French Polynesia: Mangareva Island	1	OR864762	De Mazancourt et al. (2024)
	French Polynesia: Rapa Island	1	OR864764	De Mazancourt et al. (2024)
	French Polynesia: Rapa Island	1	OR864754	De Mazancourt et al. (2024)
	French Polynesia: Rapa Island	1	OR864761	De Mazancourt et al. (2024)

Pairwise distance estimates based on the K2P model, using the pairwise deletion option, were calculated in MEGA to assess interand intraspecific genetic diversity between the new species and other species of *Ptychognathus*. Due to the large number of species, and the considerable morphological differences between some of them and the new species, interspecific genetic diversities were calculated only by comparing the new species with morphologically similar species.

Results

Taxonomy

Family Varunidae H. Milne Edwards, 1853
Subfamily Varuninae H. Milne Edwards, 1853
Genus *Ptychognathus* Stimpson, 1858

***Ptychognathus dajie* sp. nov.**
https://zoobank.org/4A93B11E-2674-47B4-BEFA-2137407439C2
Figs 2, 3, 5A

Ptychognathus barbatus – De Man 1895: 105, fig. 23 [Indonesia: Atjeh and Ambon Island; Malaysia: Penang] (part); De Man 1898: 698, fig. 23 [Indonesia: Atjeh; Malaysia: Penang] (part); De Man 1902: 505 [Indonesia: Ternate]; Tesch 1918: 87 (key) (part?); Maki and Tsuchiya 1923: 188 [Taiwan]; Tweedie 1936: 50 [Malaysia: Tioman Island]; Sakai 1939: 659, text-fig. 113 [Japan: Ryukyu Islands]; Lin 1949: 28 [Taiwan]; Sakai 1976: 638, text-fig. 348, pl. 219(2) [Japan: Ryukyu Islands]; Dai et al. 1986: 468, fig. 262, pl. 65(8) [China: Guangdong]; Fukui et al. 1989: 229, fig. 14 [Taiwan]; Dai and Yang 1991: 515, fig. 262, pl. 65(8) [China: Guangdong]; Wang and Liu 1996a: 109, figs 136–137 [Taiwan]; Wang and Liu 1996b: 77, 2 unnumb. figs [Taiwan]; Jeng 1998: 123 [Taiwan]; Muraoka 1998: 52 [Japan; Taiwan]; Kato and Okuno 2001: 139, 1 unnumb.

fig. [Japan: Izu Islands]; Lee 2001: 130, 1 unnumb. fig. [Taiwan]; Kishino et al. 2001: 126 [Japan: Amami Island]; Ng et al. 2001: 46 [Taiwan] (list); Akio and Yoshihiko 2007 [Japan: Kochi and Ehime Prefectures]; Ng et al. 2008: 228 (list) (part); Naruse 2010: 54 [Japan: Okinawa Island]; Ng et al. 2017: 115 [Taiwan] (list); Toyota et al. 2019: 298, 5 unnumb. figs [Japan: Kanagawa, Ryukyu Islands, Izu Islands]; Wada 2021: 107 [Taiwan]; Sasaki 2023: 15534 (list) (part). non *Ptychognathus barbatus* A. Milne-Edwards, 1873.

Ptychognathus aff. *barbatus* – Hsu and Shih 2020: 7, tab. 1 [Taiwan; Indonesia: Bali Island]; Hsu et al. 2022: 8 [Taiwan] (key); Hsu and Shih 2024a: 160, tab. 2 [Taiwan].

Cognatus cavaterminus NK Ng, 2006: 387, figs 107, 108 (unpublished MS name), nomen nudum.

Cognatus benokiensis NK Ng, 2006: 392 (unpublished MS name), nomen nudum.

Type material. ***Holotype*.** Malaysia • 1 male (13.2 × 11.6 mm); Pahang, Tioman Island, Paya River; 7–12 Sep. 2002; ZRC 2024.0072. ***Paratypes*.** Malaysia • 19 males (14.8 × 13.0–6.9 × 6.1 mm), 22 females (10.9 × 9.4–5.2 × 4.1 mm), 2 ovig. females (8.9 × 7.6, 7.3 × 7.0 mm); same as the holotype; 7–12 Sep. 2002; ZRC 1985.1569–1573. 2 males (14.8 × 13.0, 14.3 × 12.3 mm), 3 females (10.9 × 9.4, 10.6 × 9.2, 10.5 × 9.1 mm); same as the holotype; 7–12 Sep. 2002; NCHUZOOL 17356.

Other material. **Japan** • 9 males (15.5 × 13.8–9.5 × 8.8 mm), 4 females (12.0 × 11.0–9.0 × 8.4 mm), 1 ovig. female (10.8 × 9.7 mm); Ryukyu Islands, Okinawa, Miyako, Urasoko; 11 Apr. 2002; NCHUZOOL 17335. 28 males (10.0 × 8.9–4.5 × 4.0 mm); Ryukyu Islands, Okinawa, Benoki, Benoki River; 7 Jul. 1990; ZRC 2008.0035 (labeled as "*Cognatus benokiensis*" in NK Ng 2006's dissertation). **Taiwan** • 10 males (12.4 × 10.9–7.7 × 6.8 mm), 5 females (15.3 × 13.1–8.9 × 8.0 mm); Yilan, Toucheng, Dasi; 15 Aug. 2016; NCHUZOOL 16063. 2 males (14.7 × 12.9, 10.1 × 9.0 mm), 1 female (13.0 × 11.0 mm), 1 ovig. female (13.2 × 11.3 mm); Hualien, Shoufeng, Yanliao; 29 Jun. 2016; NCHUZOOL 16064. 2 females (7.4 × 6.5, 6.7 × 5.7 mm); Taitung, Donghe, Dulanwan; 9 Aug. 2017; NCHUZOOL 16065. 1 male (13.0 × 11.1 mm); Taitung, Donghe, Dulanwan; 27 Jul. 2014; NCHUZOOL 16066. 2 males (11.0 × 10.1, 11.0 × 10.0 mm), 1 female (9.4 × 8.3 mm); Taitung, Chenggong, Gihui; 28 Apr. 2017; NCHUZOOL 16067. 3 males (14.9 × 12.7–12.1 × 10.8 mm); Changhua, Fubao; 16 Jan. 2017; NCHUZOOL 16075. 2 males (20.2 × 16.8, 18.9 × 16.2 mm), 1 female (11.5 × 10.3 mm); Kaohsiung, Linyuan, Gaoping R. estuary; 29 Apr. 2009; NCHUZOOL 16074. 4 males (16.9 × 14.7–9.9 × 8.9 mm), 1 female (8.6 × 7.7 mm); Pingtung, Hengchun, Houwan; 11 Jul. 2017; NCHUZOOL 16073. 6 males (10.1 × 9.0–5.7 × 5.0 mm), 1 female (10.0 × 9.1 mm), 1 ovig. female (11.0 × 10.0 mm); Pingtung, Hengchun, Houwan; 22 Sep. 2021; NCHUZOOL 17343. 1 male (13.0 × 11.4 mm); Pingtung, Checheng, Baoli R. estuary; 23 June 2014; NCHUZOOL 16072. 8 males (13.1 × 11.3–9.3 × 8.2 mm), 3 females (11.9 × 10.6–8.8 × 7.7 mm), 2 ovig. females (9.7 × 8.7, 8.2 × 7.1 mm); Pingtung, Hengchun, Wanlitong; 11 Dec. 2018; NCHUZOOL 16070. 3 males (13.9 × 12.0–12.6 × 10.9 mm), 1 female (9.0 × 8.1 mm), 1 ovig. female (11.1 × 9.6 mm); Pingtung, Hengchun, Wanlitong; 13 Mar. 2021; ZRC 2022.0839. 15 males (13.0 × 11.4–7.8 × 7.1 mm), 4 females (13.6 × 11.7–9.3 × 8.4 mm), 2 ovig. females (12.5 × 10.9, 7.7 × 7.0 mm); Pingtung, Hengchun, Wanlitong; 13 Mar. 2021; NCHUZOOL 17342. 5 males (11.4 × 10.2–7.8 × 7.1 mm), 1 female (9.4 × 8.4 mm); Pingtung, Hengchun, Dingtanzih; 19 Mar. 2018; NCHUZOOL

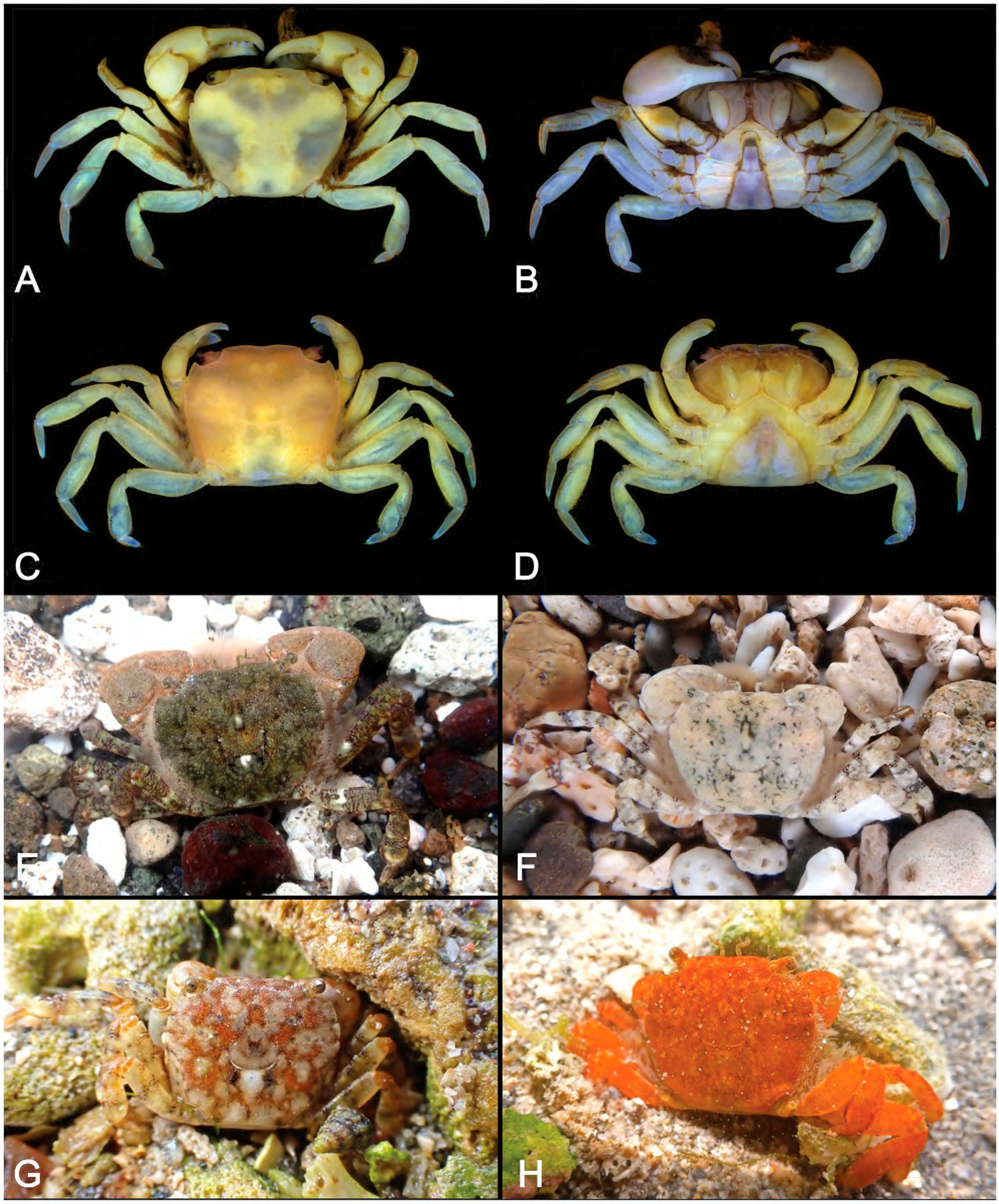

Figure 2. *Ptychognathus dajie* sp. nov. **A, B.** Holotype male (13.2 × 11.6 mm, ZRC 2024.0072); **C, D.** Paratype female (10.6 × 9.2 mm, NCHUZOOL 17356); **E.** Male (NCHUZOOL 17341); **F.** Male (NCHUZOOL 17343); **G, H.** Males (NCHUZOOL 17342). **A, C.** Dorsal view; **B, D.** Ventral view; **A–D.** Preserved specimens; **E–H.** Color in life.

16071. 3 males (10.5 × 9.4–6.5 × 5.8 mm), 1 female (8.9 × 7.9 mm); Pingtung, Hengchun, Gangkou R. estuary; 18 Aug. 2016; NCHUZOOL 16069. 1 male (14.7 × 12.8 mm); Pingtung, Manjhou, Jhonggang R. estuary; 7 Nov. 2018; NCHUZOOL 16068. 2 males (14.0 × 12.3, 7.0 × 6.3 mm), 1 female (10.8 × 9.7 mm);

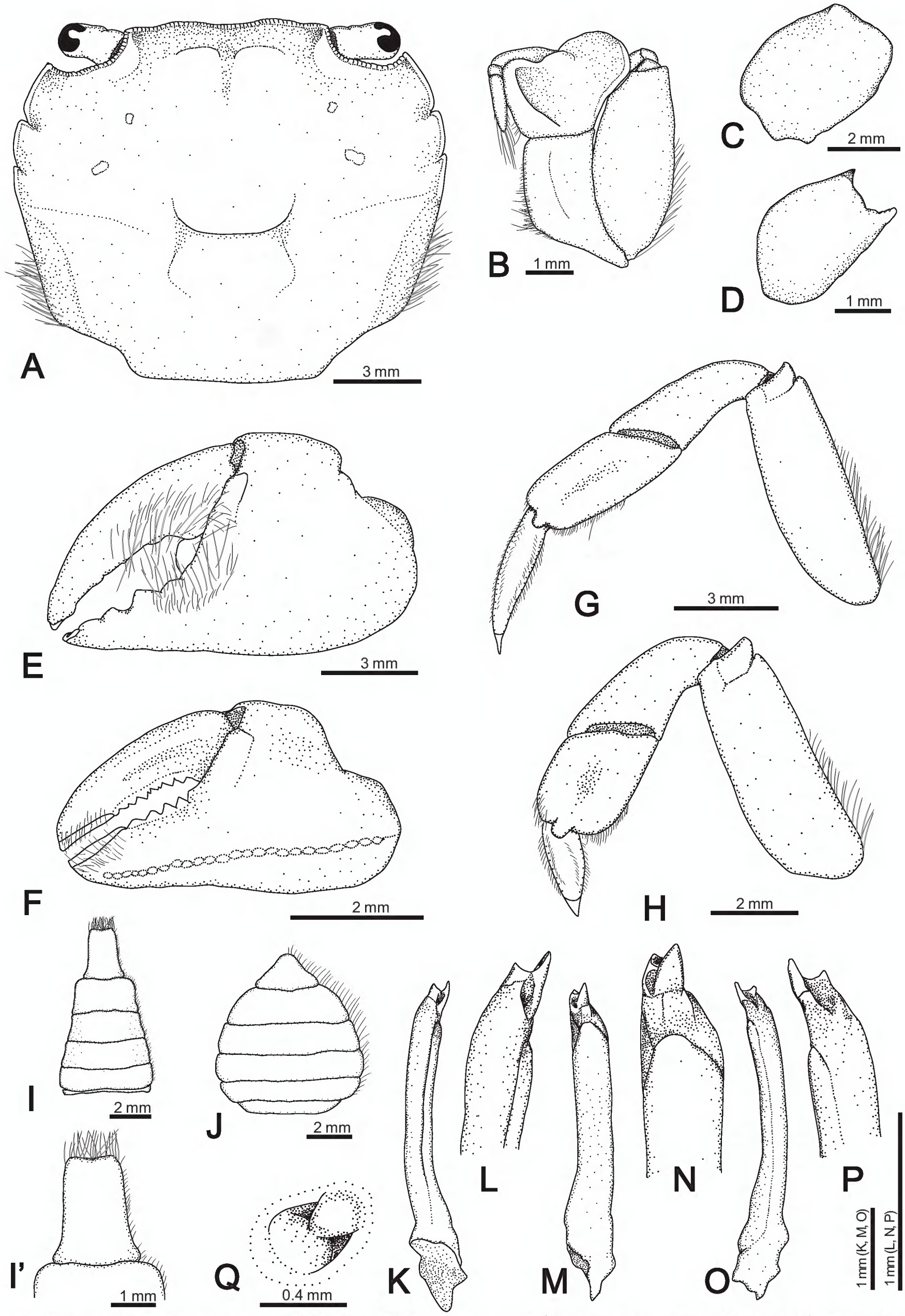

Figure 3. *Ptychognathus dajie* sp. nov. **A–C, E, G–I, K–P.** Holotype male (13.2 × 11.6 mm, ZRC 2024.0072); **D, F, J, Q.** Paratype female (10.6 × 9.2 mm, NCHUZOOL 17356). **A.** Carapace; **B.** Left third maxilliped; **C, D.** Left carpus of cheliped (dorsal view); **E, F.** Outer view of left cheliped; **G.** left third ambulatory leg (P4); **H.** Left forth ambulatory leg (P5); **I, J.** Pleon; **I'.** telson; **K, L.** Right G1 (dorsal view); **M, N.** Right G1 (lateral view); **O, P.** Right G1 (ventral view); **Q.** Right vulva.

Penghu Islands, Baisha, Watong; 2 Sep. 2014; NCHUZOOL 16076. 2 males (14.5 × 12.8, 9.3 × 8.6 mm), 2 females (14.2 × 12.7, 11.3 × 10.3 mm); Lanyu Island, Yeyou; 13 Mar. 2023; NCHUZOOL 17341. **Philippines** • 5 males (15.3 × 13.7–11.2 × 10.2 mm), 1 female (14.5 × 12.6 mm), 2 ovig. females (16.8 × 14.5, 13.6 × 12.1 mm); Camiguin Island; 30 Aug. 2003; NCHUZOOL 17336. **Indonesia** • 1 ovig. female (8.1 × 7.2 mm); Bali Island; 18 Jul. 2014; NCHUZOOL 16504.

Comparative material. *Ptychognathus amikee* Hsu & Shih, 2024: VANUATU • 1 male (holotype, 15.8 × 13.6 mm); Gaua Island, Kirilou River; 18 Jul. 2005; MNHN-B29852. 1 female (paratype, 17.4 × 14.6 mm), Gaua Island, Lembot River; 20 July 2005; MNHN-B29853. *Ptychognathus barbatus* (A. Milne-Edwards, 1873): FRANCE • 4 males (10.2 × 8.5–8.6 × 7.3 mm), 3 females (8.5 × 6.9–7.0 × 6.1 mm); New Caledonia; 8 Nov. 2006; ZRC 2019.1806. *Ptychognathus glaber* Stimpson, 1858: Japan • 2 males (11.4 × 9.5, 10.6 × 8.6 mm), 2 females (11.4 × 9.6, 11.0 × 9.1 mm); Ogasawara Islands, Chichi-jima Island, Futami, Kiyose River; 10 Dec. 2005; ZRC 2023.0086. *Ptychognathus guijulugani* Rathbun, 1914: Indonesia • 14 males (9.1 × 7.9–6.6 × 5.8 mm), 6 females (8.9 × 7.4–5.9 × 5.2 mm) 2 ovig. females (7.2 × 6.3, 6.9 × 6.2 mm); Bali Island; 18 Jul. 2014; NCHUZOOL 17334. *Ptychognathus hachijoensis* Sakai, 1955: Taiwan • 4 males (9.8 × 7.7–7.0 × 5.9 mm), 6 females (8.0 × 6.7–6.3 × 5.4 mm); Hualien, Shoufeng, Yanliao; 29 Jun. 2016; NCHUZOOL 15809. *Ptychognathus insolitus* Osawa & NK Ng, 2006: Taiwan • 1 male (9.1 × 6.3 mm), 2 females (7.9 × 6.0, 5.8 × 4.6 mm); Taitung, Donghe, Dulanwan; 29 Jun. 2016; NCHUZOOL 16041. *Ptychognathus ishii* Sakai, 1939: Taiwan • 2 males (11.4 × 8.8, 8.9 × 7.3 mm), 2 females (9.1 × 8.6, 8.9 × 7.1 mm); Yilan, Toucheng, Dasi; 16 Aug. 2016; NCHUZOOL 16034. *Ptychognathus lipkei* NK Ng, 2010: Philippines • 4 males (paratypes, 14.6 × 11.6–11.0 × 9.2 mm); Cebu Island, Matutinao, Matutinao River mouth, Kawasan Falls; 30 Jul. 2003; ZRC 2013.1823. *Ptychognathus pusillus* Heller, 1865: AUSTRALIA • 2 males (13.2 × 11.3, 10.5 × 9.2 mm), 2 females (14.2 × 12.0, 13.2 × 11.3 mm); Christmas Island, Dolly Beach; 29 Jan. 2010; ZRC 2023.1844. *Ptychognathus sakaii* Hsu, Shih & Li, 2022: Taiwan • 1 male (holotype, 6.7 × 5.5 mm); Pingtung, Hengchun, Dingtanzih; 3 Apr. 2019; NCHUZOOL 17047. 3 males (paratypes, 6.7 × 5.5–5.7 × 5.0 mm), 1 ovig. female (5.9 × 5.2 mm); Pingtung, Hengchun, Dingtanzih; 3 Apr. 2019; NCHUZOOL 16503. *Ptychognathus stimpsoni* Hsu & Shih, 2020: Taiwan • 1 male (holotype, 7.9 × 6.6 mm); Pingtung, Hengchun, Wanlitong; 15 Aug. 2016; NCHUZOOL 16501. Philippines • 16 males (paratypes, 10.9 × 9.0–7.3 × 6.2 mm), 4 females (8.8 × 7.2–7.5 × 6.3 mm); Camiguin Island; 31 Aug. 2003; NCHUZOOL 16502. *Ptychognathus takahasii* Sakai, 1939: Taiwan • 4 males (10.1 × 8.6–8.9 × 7.8 mm), 2 females (9.7 × 8.5, 7.0 × 6.3 mm), 2 ovig. females (8.9 × 7.7, 8.0 × 6.9 mm); Taitung, Chenggong, Gihui; 28 Apr. 2017; NCHUZOOL 16058.

Diagnosis. Carapace (Figs 2A, C, 3A) subquadrate (CW/CL ~ 1.1–1.2); dorsal surface glabrous. Front broad, frontal margin concave medially, slightly divided into two indistinct lobes; postfrontal region distinct, separated into two lobes by shallow grooves. Anterolateral margin with three teeth including orbital tooth, third tooth small but distinct. Exopod of third maxilliped (Figs 2B, D, 3B) ~ 1.3 × as wide as ischium. Chelipeds (Fig. 2) symmetrical; inner angle of male carpus (Fig. 3C) without spines; inner surface of palm glabrous; in male (Fig. 3E), proximal 1/2 of fingers with tufts of long dense soft setae on outer surface, slightly extending to palm side; base of fingers with pulvinus in male; setae and pulvinus absent in female (Fig. 3F). P4 (Figs 3G, 5A) merus densely

invested with long setae on proximal 1/2–2/3 of anterior margin; propodus densely invested with short setae on distal 1/3–1/2 of posterior margin and of distal anterior margin, with sparsely scattered long setae; dactylus densely invested with short setae on most of anterior and posterior margins. P5 (Figs 3H, 5A) merus with densely covered with long setae on proximal 2/3–3/4 of anterior margin; propodus densely covered with short setae on distal 1/3–1/2 of posterior margin and distal anterior margin, with sparsely scattered long setae; dactylus densely invested with short setae on almost entire anterior and posterior margins, denser on anterior margin. Male pleon (Fig. 3I) narrow, distal margin of telson concave with tuft of setae. G1 (Fig. 3K–P) slender, distally slightly curved toward dorsolateral side; tip chitinous, with truncated lobe in lateral view, curved toward dorsolateral side, two angles strongly prominent.

Description. Carapace (Figs 2A, C, 3A) subquadrate, 1.1–1.2 × (*n* = 127) as wide as long; dorsal surface flat, finely punctate, glabrous; regions weakly defined, with noticeable groove between epigastric regions; hepatic region smooth, without small granules; metabranchial region sloping outwards. Front broad, slightly convex near orbital regions; frontal margin concave medially, lined with small, rounded granules, slightly divided into two indistinct lobes; postfrontal region distinct, separated into two lobes by shallow grooves.

Supraorbital margins lined with small granules. Anterolateral margin with three teeth including external orbital tooth; first tooth (external orbital tooth) largest, broad, bluntly triangular, slightly sloping forward; second tooth distinct, bluntly triangular; third tooth smallest, sometimes small but distinct or indicated by a small notch in small individuals. Posterolateral margins convergent posteriorly, covered with dense setae; posterolateral regions covered with dense setae near margins. Infraorbital ridge consisting of several small, rounded granules. Epistome broad, median part triangular.

Third maxillipeds (Figs 2B, D, 3B) broad, external surface almost glabrous; merus with shallow oblique groove along mesial margin of external surface, anterolateral angle broadly rounded, sloping laterally; ischium with an indistinct shallow groove slightly mesial to midline of external surface; exopod broad, convex, ~ 1.3 × as wide as ischium.

Chelipeds (Fig. 2) symmetrical in male and female, typically larger in male. Inner angle of carpus (Fig. 3C) without spines in male (with small distinct spine in female; Fig. 3D). Inner surface of palm glabrous; in male (Fig. 3E), proximal 1/2 of fingers with tufts of long dense soft setae on outer surface, slightly extending to palm side; base of fingers with pulvinus in male; in female (Fig. 3F), outer surface of palm glabrous and slightly granulated, inner surface glabrous; immovable finger with ridge consisting of small granules toward palm, fingers with short setae at tips; base of fingers without pulvinus.

Ambulatory legs (Figs 2, 3G, H, 5A) slender, P3 and P4 almost equal in length, longest, P5 shortest; setation not different between male and female. Meri without spines, but with long soft setae on proximal 1/2–2/3 of anterior margin; posterior margins almost glabrous; dorsal surfaces almost glabrous. P2 (Fig. 2) relatively short; propodus covered with dense short setae on anterior margin and ventral surface; dorsal surface glabrous, anterior margin of distal half densely covered with short setae; dactylus covered with rows of short setae on margins and surface. P3 and P4 (Figs 2, 3G, 5A) relatively long; meri ~ 2.9 × as long as wide (holotype); carpi glabrous on margins and surfaces; propodi

~ 2.2 as long as wide (holotype), dorsal surface glabrous, with dense short and sparse long setae on distal 1/3–1/2 of posterior margin and distal anterior margin (denser on distal part); dactyli almost equal to propodi in length, with dense short setae on anterior and posterior margins. P5 (Figs 3H, 5A) relatively short; merus ~ 2.8 × as long as wide (holotype); carpus glabrous on margins and surfaces; propodus ~ 1.4 × as long as wide (holotype), dorsal surface glabrous, with dense short and sparse long setae on distal 1/3–1/2 of posterior margin and distal anterior margin (denser on distal part); dactylus with dense short setae on almost entire anterior and posterior margin, denser on anterior margin.

Male pleon (Fig. 3I) narrow; external surface smooth, without any granules; lateral margins lined with short setae; telson subrectangular, significantly longer and narrower than sixth pleonal somite, distal margin concave, with a tuft of setae. Female pleon (Fig. 3J) wide; external surface smooth, without any granules; lateral margins lined with short setae; telson bluntly triangular, almost equal to sixth pleonal somite in length.

G1 (Fig. 3K–P) slender, distally slightly curved toward dorsolateral side; tip chitinous, with truncated lobe in lateral view, curved toward dorsolateral side, two angles strongly prominent; G2 shorter than 1/4 length of G1.

Female vulvae (Fig. 3Q) with one elongated short and one rounded sternal vulvar covers; sunken on mesial part.

Color in life. The coloration of this new species is highly variable, so color is not a reliable characteristic for identification. The body color often resembles the color of the habitat substrate. Common body colors include dark brown or grayish black (Fig. 2E) or ivory white (Fig. 2F), with occasional individuals appearing in pale brown or orange (Fig. 2G, H). The carapace frequently has scattered spots, and the ambulatory legs often exhibit banding (e.g., Fig. 2E–G). The preserved specimens examined are pale brown.

Ecology. This species primarily inhabits estuaries or freshwater downstream areas influenced by tide, often sheltering under stones or pebbles in shallow waters or near the water. Its habitat is diverse, including sandy bottoms, coral sand, and rocky shores. *Ptychognathus dajie* sp. nov. frequently coexists with other *Ptychognathus* species in similar habitat environments. In Taiwan, this species has been observed to be sympatric with several species, such as *P. insolitus*, *P. ishii*, *P. lipkei*, *P. sakaii*, *P. stimpsoni*, and *P. takahasii*.

Size. Largest male 20.2 × 16.8 mm (NCHUZOOL 16074); largest female 16.8 × 14.5 mm (NCHUZOOL 17336); smallest ovig. female 7.7 × 7.0 mm (NCHUZOOL 17342).

Distribution. Malaysia (Tioman) (type locality), Japan (Kochi, Ehime, Kanagawa, Izu Islands, and Ryukyu Islands), Taiwan, China (Guangdong), the Philippines (Negros, Cebu, and Camiguin), Indonesia (Sumatra, Ternate, and Bali Island); and Thailand (Phuket) (De Man 1898, 1902; Dai and Yang 1991; Ng 2006; Sasaki 2023; present study) (Fig. 1).

Etymology. The species is named in honor of the late Dr. Ngan Kee Ng, who focused on this varunid group as part of her doctoral research. The specific epithet *dajie*, in Chinese, is a form of address to a senior woman in a leadership or caretaker role, similar to “big sister” or “senior sister”. Used as a noun in apposition.

Remarks. *Ptychognathus dajie* sp. nov. is morphologically similar to a group of species within *Ptychognathus*, viz. *P. barbatus*, *P. glaber*, *P. guijulugani*, *P. ngankeeae* De Mazancourt, Mazel, Marquet, Poupin & Keith, 2024, *P. pusillus*,

P. sakaii, and *P. stimpsoni*, in the following features: small body size, subquadrate carapace, and ambulatory legs without densely long setae. Nonetheless, the new species can be distinguished from these congeners primarily by the shape of the male telson and the pattern of setation in the ambulatory legs and male telson. The morphology of the male telson in *P. dajie* sp. nov., in particular, is rather unique in the genus in that the distal margin of male telson is obviously concave and with a distinct tuft of setae (Figs 2B, 3I) (vs neither concave nor truncated and without tufts of setae in other species). There is, however, no obvious interspecific difference in female telsons. Moreover, based on the unique morphology of the male telson in this species, Hsu and Shih (2020) also recognized it as distinct from *P. barbatus* and referred to it as *P.* aff. *barbatus*.

Ptychognathus dajie sp. nov. can be further differentiated from other congeners by the form of the carapace and the setation of the ambulatory legs. In *P. dajie* sp. nov., there are three obvious anterolateral teeth (including the external orbital tooth) on the carapace, and the second tooth is distinct and bluntly triangular (Fig. 3A) (vs single tooth and 1 or 2 notches or weak teeth in *P. glaber* and *P. sakaii*; Komai et al. 2021: figs 1A, 2A; Hsu et al. 2022: figs 1A, 2A).

Although *P. dajie* sp. nov. and four other closely allied species (*P. barbatus*, *P. guijulugani*, *P. pusillus*, and *P. stimpsoni*) all have a similar carapace, including shape and anterolateral teeth morphology, they can be distinguished by the setation of the ambulatory legs. In *P. stimpsoni*, the surface near the anterior margins of the ambulatory carpi and propodi is covered with dense, short setae (Hsu and Shih 2020: figs 1C–F, 4G, H) (vs not covered with dense setae in *P. dajie*, *P. barbatus*, *P. guijulugani*, *P. ngankeeae*, and *P. pusillus*; Figs 2, 3G, H, 4, 5; see Tesch 1918: pl. 4, fig. 6; De Man 1905: pl. 17, fig. 1; De Mazancourt et al. 2024: figs 11E, F, 12A, C, 13E, F). There are five species within *Ptychognathus*, including *P. barbatus*, *P. guijulugani*, *P. ngankeeae*, *P. pusillus*, and *P. dajie* sp. nov., have very similar morphologies in the carapace, chelipeds, and shape of ambulatory legs; they can be discriminated by male pleons, the setation of ambulatory legs, and G1s (Table 2). In *P. dajie* sp. nov., as mentioned above, the distal margin of male telson is distinctly concave, with a distinct tuft of setae (Figs 2B, 3I) (vs not concave and without distinct tuft of setae in other four species; Fig. 4B, D, F; see De Mazancourt et al. 2024: fig. 13G). In term of the setation of ambulatory legs, there are some differences between these five species: a) in *P. dajie* sp. nov., the anterior margin of the P4 propodus bears setae only on the distal part, while the rest of the margins are almost glabrous (Figs 2, 3G, 5A) [vs almost whole anterior margin covered with setae, denser in distal part in *P. barbatus*; Figs 4A, B, 5B; see De Mazancourt et al. 2024: fig. 11E); the anterior margins are almost glabrous in *P. guijulugani*, *P. ngankeeae*, and *P. pusillus* (Figs 4C–F, 5C, D; see De Mazancourt et al. 2024: fig. 13E)]; b) in three species (*P. dajie* sp. nov., *P. ngankeeae* and *P. pusillus*), the P5 propodi bear short setae on distal 1/3–1/2 of posterior margins, and distal anterior margins (Figs 2, 3H, 4E, F, 5A, D; see De Mazancourt et al. 2024: fig. 13F) [vs with short setae on distal 1/3–1/2 of posterior margin, and distal 1/2–2/3 anterior margin in *P. barbatus* (Figs 4A, B, 5B; see De Mazancourt et al. 2024: fig. 11F); with dense long setae on distal 1/2–2/3 of posterior margin, and with short setae on distal anterior margin in *P. guijulugani* (Figs 4C, D, 5C)]. In addition, the chitinous structure of G1 are also different: in *P. dajie* sp. nov., the chitinous structure is a truncated lobe in lateral view, and the two angles are strongly prominent (Fig. 3K–P) [vs chitinous structure bluntly

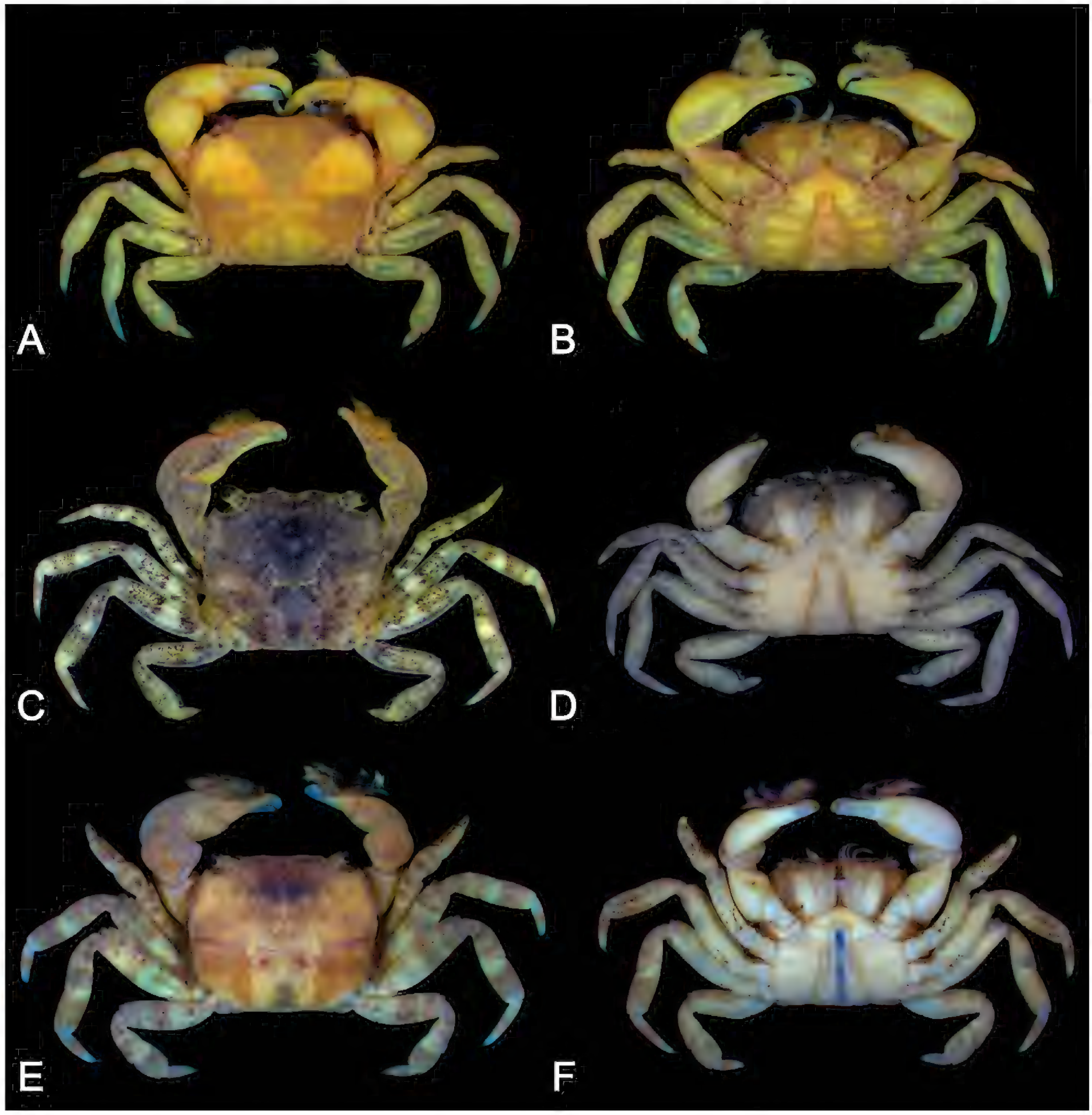

Figure 4. Three species of *Ptychognathus*. **A, B.** *Ptychognathus barbatus* (A. Milne-Edwards, 1873) (male, CW 10.2 mm, ZRC 2019.1806); **C, D.** *Ptychognathus guijulugani* Rathbun, 1914 (male, CW 8.8 mm, NCHUZOOL 17334); **E, F.** *Ptychognathus pusillus* Heller, 1865 (male, CW 13.2 mm, ZRC 2013.1844). **A, C, E.** Dorsal view; **B, D, F.** Ventral view.

Table 2. Comparison of characters of five species of *Ptychognathus*.

Character	*P. dajie* sp. nov.	*P. barbatus*	*P. guijulugani*	*P. ngankeeae*	*P. pusillus*
Male telson (distal margin)	concave, with distinct tuft of setae (Figs 2B, 3I, I')	not concave, without tufts of setae (Fig. 4B)	not concave, without tufts of setae (Fig. 4D)	not concave, without tufts of setae (De Mazancourt et al. 2024: fig. 13G)	not concave, without tufts of setae (Fig. 4F)
P4 anterior margin	setae only on the distal part, rest almost glabrous (Figs 3G, 5A)	setae on almost whole margin, denser in distal part (Fig. 5B)	almost glabrous (Fig. 5C)	almost glabrous (De Mazancourt et al. 2024: fig. 13E)	almost glabrous (Fig. 5D)
P5 anterior margin	setae only on distal part (Figs 3H, 5A)	setae on distal 1/3–1/2 (Fig. 5B)	setae only on distal part (Fig. 5C)	setae only on distal part (De Mazancourt et al. 2024: fig. 13F)	setae only on distal part (Fig. 5D)
P5 posterior margin	short setae (Figs 3H, 5A)	short setae (Fig. 5B)	dense long setae (Fig. 5C)	short setae (De Mazancourt et al. 2024: fig. 13F)	short setae (Fig. 5D)
G1 (chitinous structure)	truncated, angles strongly prominent (Fig. 3K–P)	rounded, angles not prominent (Fig. 6A, B)	truncated, angles slightly prominent (Fig. 6C, D)	rounded, angles not prominent (De Mazancourt et al. 2024: fig. 13H)	rounded, angles not prominent (Fig. 6E, F)

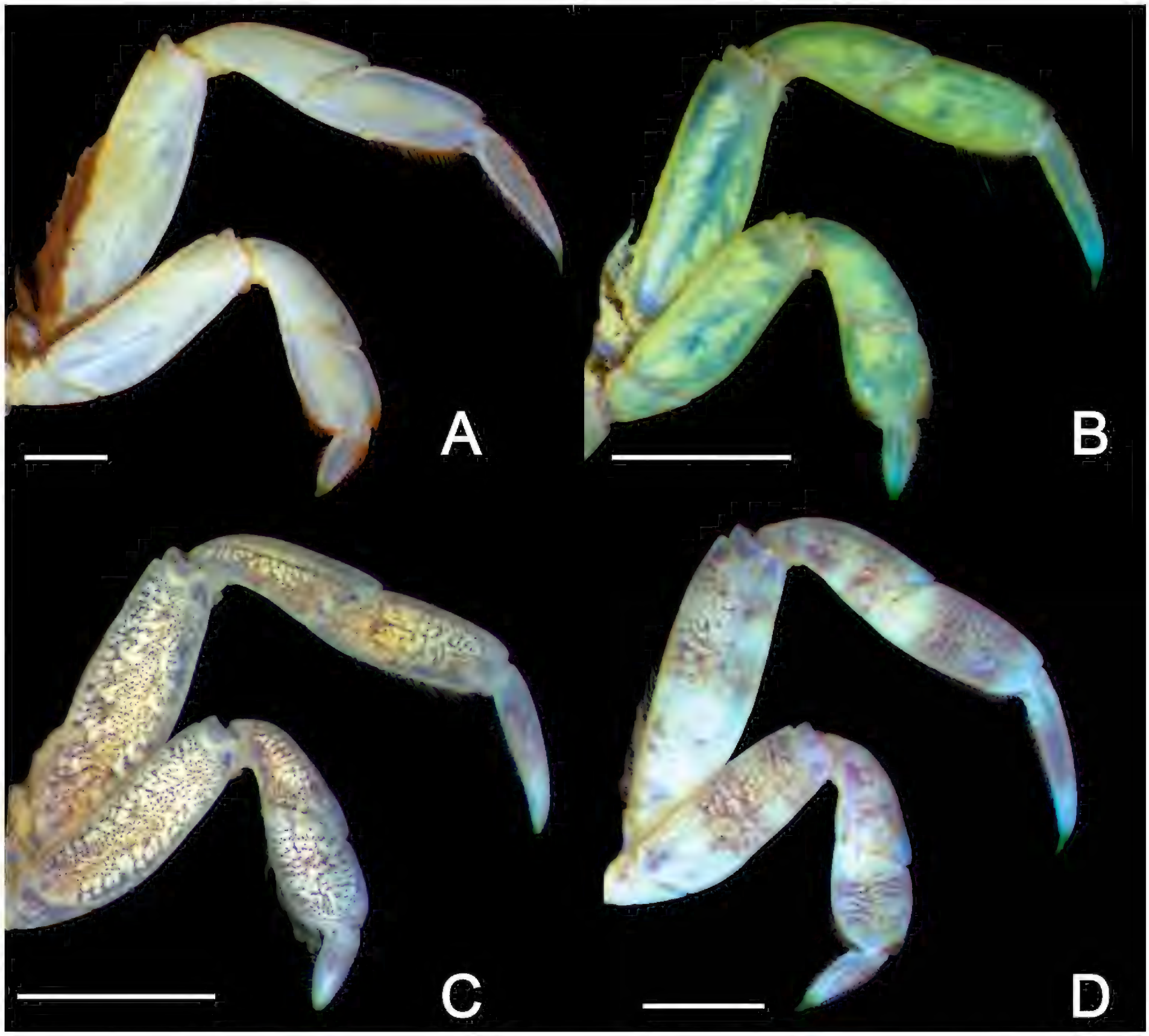

Figure 5. The right P4 and P5 of four species of *Ptychognathus* (dorsal view). **A.** *P. dajie* sp. nov. (holotype male, CW 13.2 mm, ZRC 2024.0072); **B.** *Ptychognathus barbatus* (male, CW 10.2 mm, ZRC 2019.1806); **C.** *Ptychognathus guijulugani* (male, CW 8.8 mm, NCHUZOOL 17334); **D.** *Ptychognathus pusillus* (male, CW 13.2 mm, ZRC 2013.1844). Scale bars: 3 mm.

rounded, angles not prominent in *P. barbatus*, *P. ngankeeae*, and *P. pusillus*; Fig. 6A, B, E, F; see De Mazancourt et al. 2024: figs 11I, 13H); chitinous structure truncated, two angles slightly prominent in *P. guijulugani* (Fig. 6C, D)].

DNA analyses

The NJ tree identified 21 OTUs (operational taxonomic units) with high support, corresponding to the new species in present study and 20 other previously described species (Fig. 7). The pairwise nucleotide divergences of K2P distances and bp differences of haplotypes between the new species and the 11 other species are shown in Table 3. The maximum intraspecific diversity of *P. dajie* sp. nov. is 0.77% (5 bp); while the interspecific divergences are 11.89–15.81% (71–102 bp) between *P. dajie* sp. nov. and the other species with similar morphologies (Table 3). The minimum interspecific distance (11.89%, 71 bp, between *P. dajie* sp. nov. and *P. pusillus*) is higher than those of several taxa of intertidal

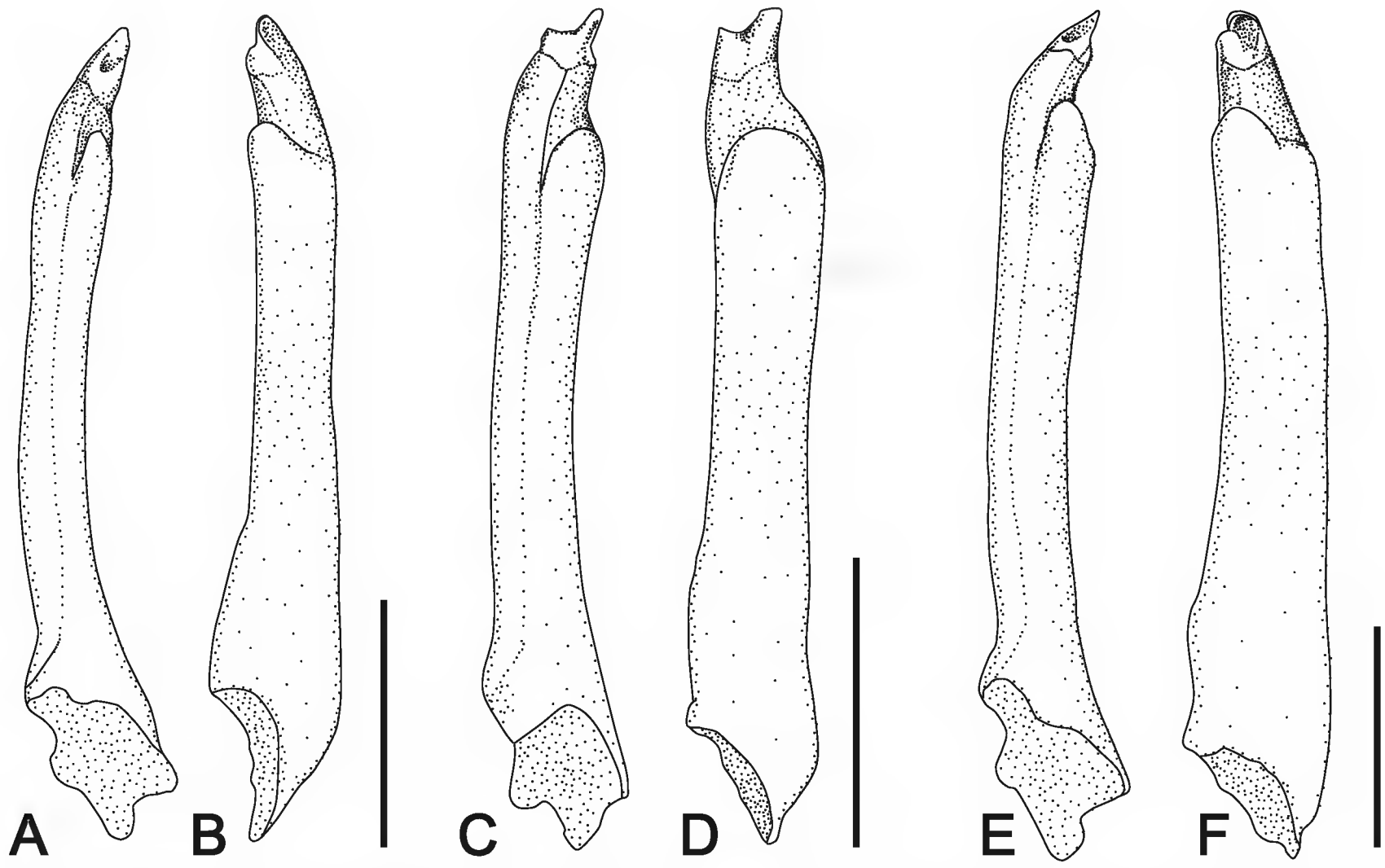

Figure 6. The right G1s of three species of *Ptychognathus*. **A, B.** *Ptychognathus barbatus* (male, CW 10.2 mm, ZRC 2019.1806); **C, D.** *Ptychognathus guijulugani* (male, CW 8.8 mm, NCHUZOOL 17334); **E, F.** *Ptychognathus pusillus* (male, CW 13.2 mm, ZRC 2013.1844). **A, C, E.** Dorsal view; **B, D, F.** Lateral view. Scale bars: 1 mm.

Table 3. Matrix of percentage pairwise nucleotide divergence using Kimura 2-parameter (K2P) distances and the mean numbers of base pair differences based on the cytochrome c oxidase subunit I (COI) between *P. dajie* sp. nov. and selected related species of *Ptychognathus* (see Table 1, Fig. 7). The range of values is shown in parentheses.

	P. guijulugani	*P. pusillus*	*P. amikee*	*P. hachijoensis*	*P. barbatus*	*P. stimpsoni*	*P. sakaii*	*P. takahasii*	*P. insolitus*	*P. similis*	*P. ngankeeae*
Nucleotide divergence	12.08	11.93	13.18	14.82	14.51	13.05	12.95	14.19	15.67	15.36	15.58
	(11.89–12.27)	(11.89–12.08)	(12.98–13.37)	(14.16–14.98)	(14.33–14.53)	(12.7–13.65)	(12.78–12.97)	(14.03–14.23)	(15.41–15.81)	(14.93–15.78)	(15.24–15.74)
bp difference	72	72.3	78.5	85.9	85	78.8	77	84.1	91.2	85.7	89
	(71–73)	(71–82)	(77–83)	(82–87)	(84–88)	(76–88)	(76–78)	(83–87)	(90–92)	(76–91)	(83–102)

crabs, including some genera in Varunidae, such as *Pseudohelice* Sakai, Türkay & Yang, 2006 (1.54%; Prema et al. 2022), *Helice* De Haan, 1833 (excluding *H. latimera* complex, 2.97%; Ng et al. 2018), *Parahelice* Sakai, Türkay & Yang, 2006 (excluding between *Par.* sp. 1 and *Par.* sp. 2, 8.2%; Hsu and Shih 2024c), *Parapyxidognathus* Ward, 1941 (10.17%; Hsu and Shih 2024b), and some other genera in other families, such as *Parasesarma* De Man, 1895 (0.92%, Sesarmidae Dana, 1851; Shih et al. 2023), *Tuerkayana* Guinot, NK Ng & Rodríguez Moreno, 2018 (1.23%, Gecarcinidae MacLeay, 1838; Ng and Shih 2023), *Minuca* Bott, 1954 (4.61%, Ocypodidae Rafinesque, 1815; Thurman et al. 2023), and *Macromedaeus* Ward, 1942 (9.7%, Xanthidae MacLeay, 1838; Yuan et al. 2022).

Among all *Ptychognathus* species, based on the constructed phylogenetic tree and calculated genetic distances, *P. dajie* sp. nov. is most closely related to *P. guijulugani* and *P. pusillus* (Fig. 7, Table 3). These three species also share similar characters, such as the structure of the carapace (Figs 2, 3A, 4C–F) and ambulatory legs (Figs 3G, H, 5A, C, D). According to the NJ tree (Fig. 7), *P. guijulugani* is the sister species of *P. dajie* sp. nov., although the support value is not high, and its G1 morphology resembles that of *P. dajie* sp. nov. more

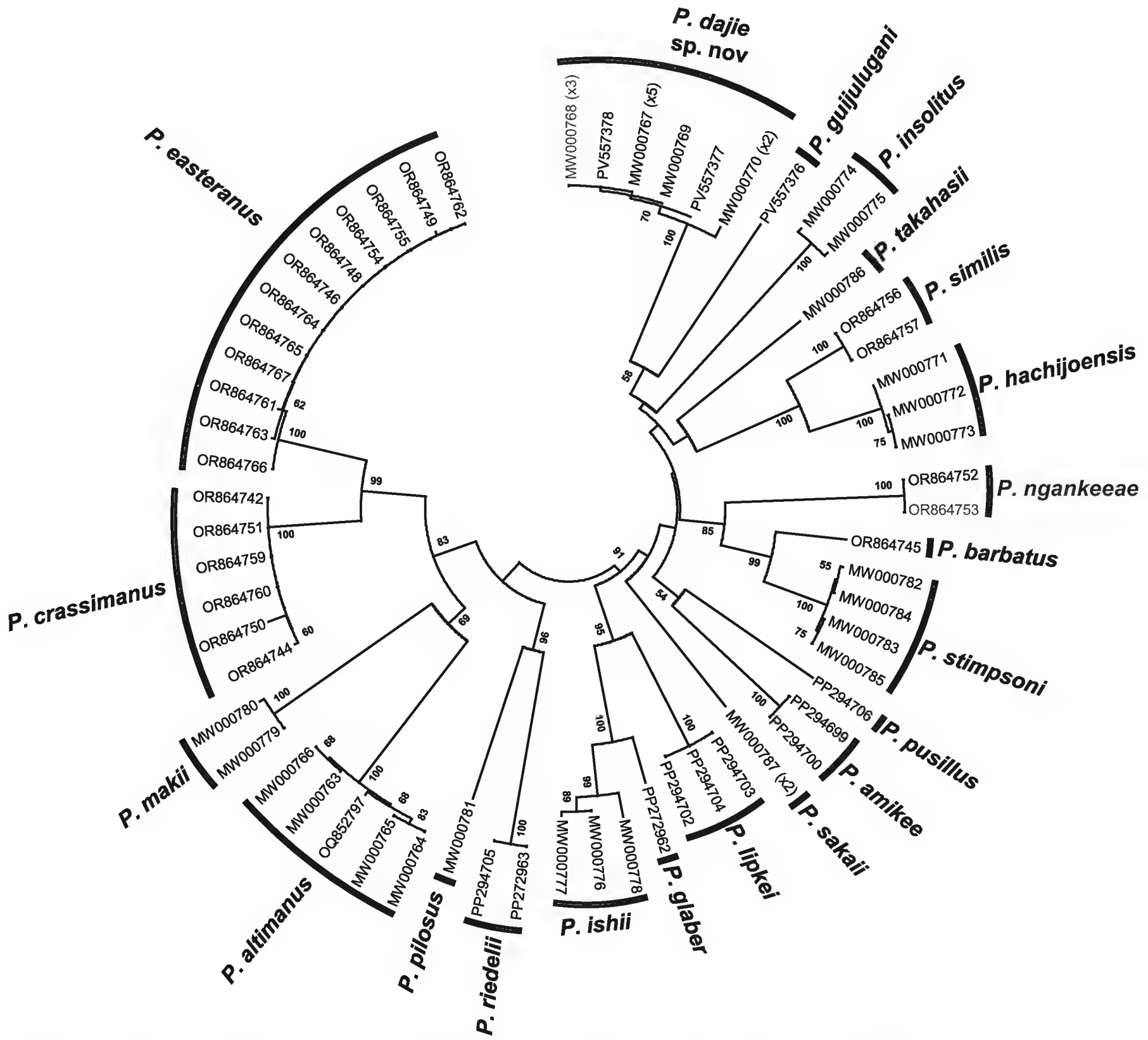

Figure 7. A neighbor-joining tree for species of *Ptychognathus*, based on the COI gene. Probability values at the nodes represent support values. Only values > 50% are shown. For haplotype names, see Table 1.

closely than that of other *Ptychognathus* species (Figs 3K–P, 6C, D). These observations suggest that species with closer phylogenetic relationships in *Ptychognathus* tend to exhibit more similar morphologies.

Discussion

Previous records of "*Ptychognathus barbatus*" from East and Southeast Asia (e.g., De Man 1902; Sakai 1939; Dai and Yang 1991, etc.) have accompanying descriptions and/or images indicating that these specimens may actually represent *P. dajie* sp. nov. rather than *P. barbatus* s. str. De Man (1902: 505) noted that the telson in male specimens from Atjeh (Indonesia) was shorter with a rounded distal margin, whereas in specimens from Ternate (Indonesia), the telson was longer with a concave distal margin. Based on these telson characters, the specimens from Ternate should be *P. dajie* sp. nov., while the specimens from Atjeh described in De Man (1895, 1898, 1902) do not represent *P. dajie* sp. nov. (De Man 1902: 505). According to the distribution and morphology, it is inferred that De Man's Atjeh specimens may correspond to *P. pusillus*. However, Ng (2006) examined certain

Atjeh specimens (RMNH-D1228; Nationaal Natuurhistorisch Museum (formerly Rijksmuseum van Natuurlijke Historie), Leiden, The Netherlands) and confirmed that their telsons possess a concave distal margin, aligning with the morphology of *P. dajie* sp. nov., suggesting that *P. dajie* sp. nov. may also be present in Atjeh. Additionally, studies of Sakai (1939), Dai et al. (1986), Dai and Yang (1991), and Toyota et al. (2019) contain descriptions or images indicating that the male telson's distal margin in specimens identified as *Ptychognathus barbatus* is concave and bears a tuft of setae, which conforms to the morphology of *P. dajie* sp. nov.

Acknowledgements

Special thanks to Peter K. L. Ng (ZRC) for his important comments on the manuscript. We also thank the member of HTS's laboratory for collecting specimens; Min-Wan Chen for performing part of the molecular work; and Taigi Sato for assisting in obtaining part of the reference materials. We are grateful to the reviewer Tomoyuki Komai and an anonymous reviewer, as well the editor Sameer Pati, who helped improve the manuscript.

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Funding

This study was supported by a grant from the National Science and Technology Council (NSTC 112-2313-B-005-051-MY3), Executive Yuan, Taiwan, to HTS.

Author contributions

JWH performed the morphological description and the molecular analysis, and drafted the manuscript. JC performed the morphological description and drafted the manuscript. HTS performed the molecular analysis, participated in the discussion and drafted the manuscript.

Author ORCIDs

Jhih-Wei Hsu https://orcid.org/0000-0002-9353-6140
Jose Christopher E. Mendoza https://orcid.org/0000-0001-9729-5703
Hsi-Te Shih https://orcid.org/0000-0003-1317-8783

Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

References

Aiko Y, Yoshihiko M (2007) Record of a brackish water crab *Ptychognathus barbatus* from Kochi and Ehime Prefectures, southern Japan (Brachyura: Varunidae). Bulletin of the Shikoku Institute of Natural History 4: 65–67.

Dai AY, Yang SL (1991) Crabs of the China Seas. Beijing, China, China Ocean Press, 21, [+] 608 pp. [74 pls]

Dai AY, Yang SL, Song YZ, Chen GX (1986) Crabs of the China Seas. China Ocean Press, Beijing, 568 pp. [74 pls] [In Chinese]

De Man JG (1895) Bericht über die von Herrn Schiffscapitän Storm zu Atjeh, an den westlichen Küsten von Malakka, Borneo und Celebes sowie in der Java-See gesammelten Decapoden und Stomatopoden. Zweiter Theil. Zoologische Jahrbucher. Abteilung fur Systematik, Geographie und Biologie der Tiere 9: 75–218. https://doi.org/10.5962/bhl.title.16084

De Man JG (1898) Bericht über die von Herrn Schiffscapitän Storm zu Atjeh, an den westlichen Küsten von Malakka, Borneo und Celebes sowie in der Java-See gesammelten Decapoden und Stomatopoden. Sechster Theil. Zoologische Jahrbucher Abteilung fur Systematiks 10: 677–708. [pls 28–38]

De Man JG (1902) Die von Herrn Professor Kükenthal im Indischen Archipel gesammelten Dekapoden und Stomatopoden. Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft 25: 467–929. [pls 19–27] https://doi.org/10.5962/bhl.title.10409

De Man JG (1905) On species of Crustacea of the genera *Ptychognathus* Stimps. and *Palaemon* Fabr. from Christmas Island. Proceedings of the Zoological Society of London 1905: 537–550.

De Mazancourt V, Mazel V, Marquet G, Poupin J, Keith P (2024) Integrative taxonomy study of brackish water crabs of the genus *Ptychognathus* Stimpson, 1858 (Crustacea: Brachyura: Varunidae) from Polynesia, with description of two new species. Zootaxa 5476(1): 267–297. https://doi.org/10.11646/zootaxa.5476.1.23

Folmer O, Black M, Hoeh W, Lutz R, Vrijenhoek R (1994) DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. Molecular Marine Biology and Biotechnology 3: 294–299.

Fukui Y, Wada K, Wang CH (1989) Ocypodidae, Mictyridae and Grapsidae (Crustacea: Brachyura) from some coasts of Taiwan. Journal of Taiwan Museum 42: 225–238.

Hsu JW, Shih HT (2020) Diversity of Taiwanese brackish crabs genus *Ptychognathus* Stimpson, 1858 (Crustacea: Brachyura: Varunidae) based on DNA barcodes, with descriptions of two new species. Zoological Studies 59: 59. https://doi.org/10.6620/ZS.2020.59-59

Hsu JW, Shih HT (2024a) A new species of the genus *Ptychognathus* Stimpson, 1858 (Crustacea: Brachyura: Varunidae) from Vanuatu. Zootaxa 5476(1): 152–165. https://doi.org/10.11646/zootaxa.5476.1.15

Hsu JW, Shih HT (2024b) A review of the varunid crab genus *Parapyxidognathus* Ward, 1941 (Decapoda: Brachyura: Varunidae), with descriptions of two new species. Journal of Crustacean Biology 44(2): ruae022. https://doi.org/10.1093/jcbiol/ruae022

Hsu JW, Shih HT (2024c) Description of a new species of *Parahelice* Sakai, Türkay & Yang, 2006, from Sulawesi, Indonesia (Decapoda, Brachyura, Varunidae). Crustaceana 97(5–9): 961–972. https://doi.org/10.1163/15685403-bja10395

Hsu JW, Shih HT, Li JJ (2022) Description of a new species of brackish-water crab of the genus *Ptychognathus* Stimpson, 1858 (Crustacea: Brachyura: Varunidae) from southern Taiwan. Nauplius 30: e2022002. https://doi.org/10.1590/2358-2936e2022002

ICZN (International Commission on Zoological Nomenclature) (1999) International Code of Zoological Nomenclature (4th edn.). The International Trust for Zoological Nomenclature, London, [xxix +] 306 pp.

Jeng MS (1998) Shrimps and crabs of Kenting National Park. Kenting National Park, Pingtung, 134 pp. [In Chinese]

Kato S, Okuno J (2001) Shrimps and Crabs of Hachijo Island. TBS Britannica Co., Ltd., Tokyo, 157 pp. [In Japanese]

Kimura M (1980) A simple method for estimating evolutionary rates of base substitutions through comparative studies of nucleotide sequences. Journal of Molecular Evolution 16(2): 111–120. https://doi.org/10.1007/BF01731581

Kishino T, Nomoto A, Kimura S, Yonezawa T, Wada K (2001) Brachyuran crab species recordes in the brackish waters of Amami-Oshima Island, Kagoshima Prefecture, Japan. Nanki-seibutsu 43: 125–131. [In Japanese with English abstract]

Komai T, Maenosono T, Saeki T, Naruse T (2021) Redescription of the brackish water crab *Ptychognathus glaber* Stimpson, 1858 based on the topotypic material from the Ogasawara Islands and new record of *P. lipkei* N. K. Ng, 2010 from Japan (Decapoda: Brachyura: Varunidae). Zootaxa 5048(1): 58–76. https://doi.org/10.11646/zootaxa.5048.1.3

Lee JH (2001) A Field Guide to Crabs in Taiwan. Bigtrees Co., Taipei, 174 pp. [In Chinese]

Lin CC (1949) A catalogue of brachyurous Crustacea of Taiwan. Quarterly Journal of the Taiwan Museum 2: 10–33.

Maki M, Tsuchiya K (1923) A Monograph of the Decapod Crustacea of Formosa. Report, Department of Agriculture, Government Research Institute, Taihoku 3: 11, [+] 251, [+] 4 pp. [24 pls] [In Japanese]

Milne-Edwards A (1873) Recherches sur la faune carcinologique de la Nouvelle-Calédonie, II. Nouvelles Archives du Muséum d'Histoire Naturelle 9: 155–332. [pls 4–18] https://doi.org/10.5962/bhl.title.10410

Muraoka K (1998) Catalogue of the brachyuran and anomuran crabs donated by Prof. Dr. Tune Sakai to the Kanagawa Prefectural Museum. Catalogue of the Collection in the Kanagawa Prefectural Museum of Natural History 11: 1–67. [pls 1–16] [In Japanese]

Naruse T (2010) Catalogue of crustacean specimens deposited in the University Museum (Fujukan), University of the Ryukyus. Catalogues of materials deposited in the University Museum (Fujukan). University of the Ryukyus 3: 1–72. [In Japanese]

Ng NK (2006) The systematics of the crabs of the family Varunidae (Brachyura, Decapoda). PhD Thesis (unpublished), National University of Singapore, Singapore, 914 pp.

Ng NK, Naruse T, Shih HT (2018) *Helice epicure*, a new species of varunid mud crab (Brachyura, Decapoda, Grapsoidea) from the Ryukyus, Japan. Zoological Studies 57: 15. https://doi.org/10.6620/ZS.2018.57-15

Ng PKL, Shih HT (2023) *Tuerkayana latens*, a new species of land crab from French Polynesia, with a discussion on the phylogeny of the genus (Crustacea: Decapoda: Brachyura: Gecarcinidae). Zoological Studies 62: 10. https://doi.org/10.6620/ZS.2023.62-10

Ng PKL, Wang CH, Ho PH, Shih HT (2001) An annotated checklist of brachyuran crabs from Taiwan (Crustacea: Decapoda). National Taiwan Museum Special Publication Series 11: 1–86. https://doi.org/10.6532/JNTM.201712_70(3;4).01

Ng PKL, Guinot D, Davie PJF (2008) Systema Brachyurorum: Part I. An annotated checklist of extant brachyuran crabs of the world. The Raffles Bulletin of Zoology (Supplement 17): 1–296.

Ng PKL, Shih HT, Ho PH, Wang CH (2017) An updated annotated checklist of brachyuran crabs from Taiwan (Crustacea: Decapoda). Journal of the National Taiwan Museum 70(3&4): 1–208. https://doi.org/10.6532/JNTM.201712_70(3;4).01

Patel H, Mendoza JCE, Bineesh KK, Mitra S, Trivedi JN (2025) On the taxonomy of *Ptychognathus andamanicus* Alcock, 1900 (Crustacea: Decapoda: Brachyura: Varunidae) from the Andaman Islands, India. Zootaxa 5584(3): 429–436. https://doi.org/10.11646/zootaxa.5584.3.8

Prema M, Hsu JW, Shih HT, Ravichandran S (2022) First record of the genus *Pseudohelice* Sakai, Türkay & Yang, 2006 from India and description of a new pseudocryptic species (Crustacea: Brachyura: Varunidae). Zoological Studies 61: 56. https://doi.org/10.6620/ZS.2022.61-56

Sakai T (1939) Studies on the Crabs of Japan. IV. Brachygnatha, Brachyrhyncha. Vol. 3. Tokyo, Yokendo Co., Ltd, p. 365–741. [pls 42–111]

Sakai T (1976) Crabs of Japan and the Adjacent Seas. Tokyo, Kodansha Ltd., 773 pp. [251 pls]

Sasaki J (2023) The species list of Decapoda, Euphausiacea, and Stomatopoda, all of the World, version 07-8.12. Local Independent Administrative Agency, Hokkaido Research Organization, Resources Management and Enhancement Division, Abashiri Fisheries Research Institute, Fisheries Research Department, Hokkaido, Japan. https://doi.org/10.13140/RG.2.2.34899.96800

Shih HT, Prema M, Kumar AAJ, Saher NU, Ravichandran S, Odhano S, Paulay G (2022) Diversity and distribution of fiddler crabs (Crustacea: Brachyura: Ocypodidae) around the Arabian Sea. Zoological Studies 61: 65. https://doi.org/10.6620/ZS.2022.61-65

Shih HT, Hsu JW, Li JJ (2023) Multigene phylogenies of the estuarine sesarmid *Parasesarma bidens* species complex (Decapoda: Brachyura: Sesarmidae), with description of three new species. Zoological Studies 62: 34. https://doi.org/10.6620/ZS.2023.62-34

Tamura K, Stecher G, Kumar S (2021) MEGA11: Molecular Evolutionary Genetics Analysis version 11. Molecular Biology and Evolution 38(7): 3022–3027. https://doi.org/10.1093/molbev/msab120

Tesch JJ (1918) The Decapoda Brachyura of the Siboga Expedition, I. Hymenosomidae, Retroplumidae, Ocypodidae, Grapsidae and Gecarcinidae. Siboga-Expeditie Decapoda Monographieen 39: 1–148. https://doi.org/10.5962/bhl.title.10267

Thurman CL, Shih HT, McNamara JC (2023) *Minuca panema* (Coelho, 1972): Resurrection of a fiddler crab species from Brazil closely related to *Minuca burgersi* (Holthuis, 1967) (Crustacea, Decapoda, Brachyura, Ocypodidae). Zoological Studies 62: 45. https://doi.org/10.6620/ZS.2023.62-45

Toyota K, Seki S, Komai T (2019) Fresh and Brackish water Shrimps and Crabs of Japan. Midorishobo Co., Ltd., Tokyo, 339 pp. [In Japanese]

Tweedie MWF (1936) On the crabs of the family Grapsidae in the collection of the Raffles Museum. Bulletin of the Raffles Museum, Singapore 12: 44–70.

Wada K (2021) Catalogue of foreing decapod crustaceans collected by Dr. Keiji Wada donated to the Osaka Museum of Natural History. Occasional papers from the Osaka Museum of Natural History 4(4): 105–115.

Wang CH, Liu HC (1996a) Common Seashore Crabs of Taiwan. Taiwan Museum, Taipei, Taiwan. [In Chinese]

Wang CH, Liu HC (1996b) Estuarine Crabs of Taiwan. Wild Bird Society of Kaohsiung, Kaohsiung, Taiwan, 113 pp. [In Chinese]

Winarni ET, Simanjuntak SBI, Nuryanto A (2023) DNA barcoding of crustacean larvae with two new records of *Caridina gracilipes* and *Ptychognathus altimanus* in the western region of Segara Anakan lagoon in Indonesia. Biodiversitas Journal of Biological Diversity 24(1): 341–348. https://doi.org/10.13057/biodiv/d240141

Yuan Z, Jiang W, Sha Z (2022) A review of the common crab genus *Macromedaeus* Ward, 1942 (Brachyura, Xanthidae) from China Seas with description of a new species using integrative taxonomy methods. PeerJ 10: e12735. https://doi.org/10.7717/peerj.12735